GENEROUS PLAYERS

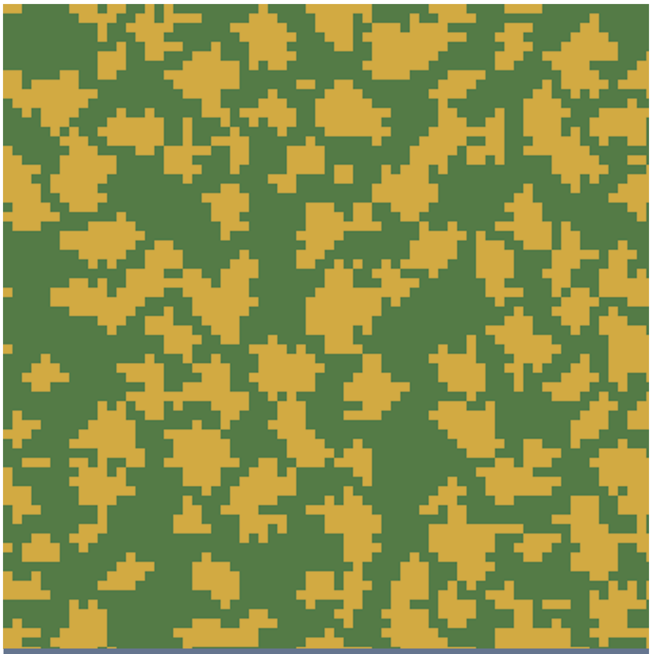
Game theory explores the Golden Rule's place in biology

BY ERICA KLARREICH

Charles Darwin's theory of natural selection seems to describe a brutal world in which creatures compete ruthlessly to promote their own survival. Yet biologists observe that animals and even lower organisms often behave altruistically. A vervet monkey who spots a leopard, for instance, warns his fellow monkeys, even though the call may attract the leopard's attention to the individual. A vampire bat that has hunted successfully shares nourishing blood with a fellow bat that failed to find prey.

Such behavior is obviously beneficial for the species as a whole. However, natural selection postulates that successful organisms act to propagate their own genes. If selfish animals can take advantage of more-generous peers, how has any generous behavior survived the mill of natural selection? Darwin himself pondered this puzzle. Focusing on human evolution, he wrote in 1871 that "he who was ready to sacrifice his life, . . . rather than betray his comrades, would often leave no offspring to inherit his noble nature."

Somehow, the altruistic behaviors observed in the wild must benefit the giver as well as the receiver. However, pinpointing how this works in animal populations is a huge challenge. In most cases, it's impossible to measure precisely how an animal's cooperative behavior affects its chances for survival and reproduction.



UNITE AND CONQUER — In a spatial version of the prisoner's dilemma, cooperators (yellow) can survive by forming clusters.

HAVERT

Now, theoretical research is starting to fill in the picture of how cooperation may survive natural selection. Some of the most illuminating ideas are coming from game theory, the field of mathematics that studies strategic behavior in competitive situations.

For decades, game theorists' basic paradigm for the puzzle of cooperation has been the scenario called the prisoner's dilemma, in which each player has a powerful incentive to exploit the other. The game is set up so that cooperation is best for the group, but each player individually does better by taking advantage of the other. A growing body of mathematical analysis and computer modeling now suggests that in many circumstances, cooperators can survive in the prisoner's dilemma. In the April 8 *Nature*, researchers argue that, under certain conditions, a cooperator can infiltrate, and eventually take over, a population of cheaters.

Meanwhile, other game theorists are arguing that the prisoner's dilemma isn't the be-all and end-all of cooperation test beds. In the same issue of *Nature*, researchers highlight another set of interactions, called the snowdrift game, in which players have incentives both to cooperate and to exploit each other. The new analysis of the snowdrift game challenges some accepted wisdom about which environmental factors encourage cooperative or exploitative behavior.

SELFISH STRATEGIES In the prisoner's dilemma, the police are separately interrogating two accomplices. Each criminal has two options: to cooperate with the other by keeping quiet or to defect by squealing on the other. If both cooperate, they'll each receive a 1-year sentence. If each incriminates the other, they'll both get 5 years. But if one cooperates and the other squeals, the cooperator will land a 10-year sentence, while the squealer will get off with only 6 months in jail.

Chase through the options, and you'll find that no matter what course one prisoner chooses, the other will do better by defecting. So, if the two players are perfectly rational, both will inevitably squeal.

The game neatly encapsulates the cooperation paradox: Even though cooperation is the best plan, it fails to be adopted, since cheating benefits the individual.

Although the prisoner's-dilemma scenario may seem artificial, many interactions of animals and other organisms may have a similar structure of rewards and penalties, some biologists and game theorists argue. In biological versions of the prisoner's dilemma, organisms are competing not for shorter prison sentences but for increased fitness and reproductive success.

It's not that a paramecium, say, mulls over possible strategies. "You don't need to assume that the players of a game are rational and are bent on out-thinking each other," says Karl Sigmund, a game theorist at the University of Vienna in Austria. "They just have to follow their inbuilt programs."

What's needed is for strategies to be predetermined by an organism's genes and inherited from one generation to the next. Then, if one strategy outperforms the others, the individuals using that strategy will tend to have more offspring, who will also follow the superior strategy. After many generations, the weaker strategies will have been weeded out, and the players will be using the strategies that rational thinkers would have come up with.

In fact, a variation on the prisoner's dilemma can take place with participants—RNA viruses—about as far removed from high-level reasoning as imaginable. In 1999, Paul Turner of Yale University and Lin Chao of the University of California, San Diego mixed two different strains of a virus called phi6. They had chosen one strain that abundantly manufactures the molecules the virus needs for reproduction, and another that puts fewer resources into making these molecules and instead grabs the molecules that the other viruses make. "They are cheaters, who exploit the viruses doing the heavy lifting," Turner says.

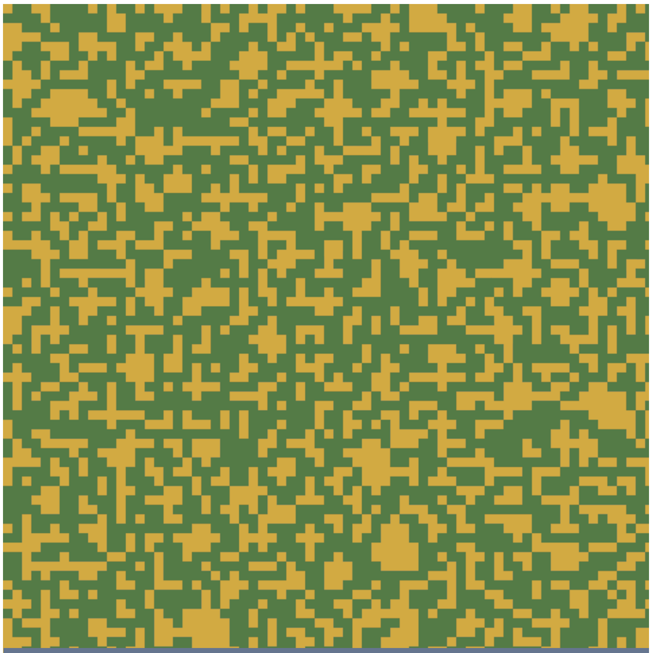
He and Chao measured how the two strains' interactions affect their fitness. "It falls out that these selfish viruses take over the system, but when that happens, the average fitness of the population drops," Turner says. "It fits in exactly with the predictions of the prisoner's dilemma."

TIT FOR TAT Things look rosier for cooperation in situations where a participant plays the prisoner's dilemma repeatedly with the same opponent and learns from previous games. After all, it can be risky to exploit someone you know you're going to encounter again.

In 1980, political scientist Robert Axelrod of the University of Michigan in Ann Arbor held a tournament in which he invited game theorists to submit strategies for repeated prisoner's-dilemma encounters. The computer-simulated tournament produced a surprise: The hands-down winner was one of the simplest strategies, a tit-for-tat rule.

A player using the tit-for-tat strategy cooperates in the first round and then in each subsequent round mimics the opponent's behavior in the previous round. In a population containing a mix of defectors and tit-for-tat players, the latter generally do better, provided there are enough of them. When they meet another tit-for-tat player, both cooperate and get a high payoff. When they meet a defector, they get suckered once, but only once. If repeatedly losing the game translates into low fitness, often the defectors do so poorly that they eventually die out, leaving an entirely cooperative population.

In 1987, Manfred Milinski of the Max Planck Institute of Limnology in Ploen, Germany, found indications that stickleback fish may play the tit-for-tat strategy during a daring maneuver called predator inspection. If a dangerous predator, such as a pike, enters the sticklebacks' neighborhood, two sticklebacks often swim together toward the open mouth of the predator, presumably to gather information on whether it poses an immediate threat.



DEFECTIVE STRATEGY — In the snowdrift game, cooperators (yellow) form tendrils, exposing themselves to defectors (green).

HAVERT

The situation looked to Milinski like a classic case of prisoner's dilemma. Cooperating—approaching the pike in synchrony—is best for the group, since it divides the risk evenly and increases the chance that at least one stickleback will survive to return to the group. Yet each individual has a strong incentive to hang back a little and let the other stickleback take more of the risk. A stickleback that lags by just half a body length cuts its risk from 50 percent to 10 percent, Milinski says.

Milinski noticed that when the sticklebacks approached the pike, one would advance a bit and then check whether the other had followed. "Each step was one round of the game," Milinski says.

To test whether the sticklebacks were using a tit-for-tat policy, Milinski placed a lone stickleback in a tank with a pike and positioned a mirror to give the stickleback the illusion that there was a second stickleback nearby. Depending on the angle of the mirror, this imaginary fish appeared to be either swimming apace or dawdling.

Milinski found that when the imaginary stickleback seemed to be defecting, the real stickleback hung back. "What the experimental fish did corresponded very well to the predicted strategy," Milinski says.

In their recent mathematical analysis reported in *Nature*, researchers have shown that a single tit-for-tat player in a population of defectors can sometimes get a toehold and then drive the defectors to extinction, provided the population is fairly small.

The researchers' reasoning goes like this. Although a single tit-for-tat player surrounded by defectors does worse than the defectors do, and so has less chance than the defectors of producing offspring, the chance is not zero. If that single player is lucky enough to have an offspring, there are now two tit-for-tat players in the population.

In a large population—say, 1 million—having a second tit-for-tat player doesn't give either one much of a boost, since their odds of running into each other are practically nil. But in a small population—say, 10—the two tit-for-tat players have an excellent chance of encountering each other, cooperating, and getting a high payoff. Depending on the particular payoffs of the game, their fitness levels may soar, and they can expect to have more offspring with each generation.

Martin Nowak of Harvard University and his collaborators have now shown that for a wide range of game parameters and population sizes, a lone tit-for-tat player actually has a better chance of its descendants eventually taking over the entire population than any individual defector does.

ANOTHER FRAMEWORK The prisoner's dilemma has long hogged the limelight when it comes to game theory as a tool to study cooperation. Christoph Hauert and Michael Doebeli of the University of British Columbia in Vancouver argue that researchers should pay more attention to the snowdrift game, which depicts a slightly less stark version of the cooperation paradox.

In this game, two cars are stuck in a massive snowdrift. Each driver can either shovel snow (cooperate) or simply sit in his car (defect). Unlike the prisoner's dilemma, in which defecting is the better strategy no matter what your opponent does, the snowdrift game requires each player to take into account the other's actions. If the other driver is shoveling, it's tempting to sit back and let him do all the work. However, if your opponent refuses to leave his car, then you'd better get out your shovel and start digging.

The snowdrift game, Hauert says, is a "promising framework for studying cooperation under less-stringent conditions than the prisoner's dilemma—ones where the cooperator gets a share of the benefits." Many animal interactions may fall into this category, he says.

Although researchers have long considered the behavior of animals and other organisms in terms of the prisoner's dilemma, few interactions have been proved conclusively to mirror that game, observes Hauert.

"I think it would be worthwhile to go through the experimental evidence [on animal interactions] again and discuss the findings with respect to the snowdrift game," Hauert says.

"Whenever nature achieves a major step, it involves cooperation."

— MARTIN NOWAK
HARVARD UNIVERSITY

In the 1970s, the father of evolutionary game theory, the late John Maynard Smith, studied the snowdrift game under a different guise, the hawk-dove game, that used a different story line but modeled the same system of rewards and punishments. Maynard Smith and the late George Price showed that cooperators and defectors coexist stably in a mix whose proportions are determined by the payoffs of the particular game. This contrasts with the prisoner's dilemma, in which cooperators die out except in special circumstances.

Curiously, the phi6 RNA viruses, which play the prisoner's dilemma in certain conditions, play the snowdrift game in others. In 2001, Turner and Chao found that if the cooperative viruses evolve in isolation before being mixed with defectors, they become so good at making the molecules needed for reproduction that they thrive even when the defectors steal molecules. Then, as in a snowdrift game, even if the cooperators do all the hard work, they're not necessarily cut down by the exploitative defectors.

NEIGHBORHOOD CONCERNS Plants and many microbial colonies and animal populations interact only with nearby organisms. In their recent *Nature* paper, Hauert and Doebeli used computer modeling to analyze what happens in the snowdrift game when players are limited to their immediate neighbors. The researchers found to their surprise that neighbor-only interactions are detrimental to cooperation in the snowdrift game.

In the prisoner's dilemma, by contrast, cooperation gets a big boost when players interact only with their neighbors. In 1992, Nowak and Robert May of Oxford University in England showed that for certain payoffs of the game, spatial structure permits cooperators to survive in protective clumps instead of dying off. By clustering, they insulate themselves from the many defectors in the population at large.

The difference between the games' outcomes arises because in the snowdrift game, but not in the prisoner's dilemma, it's in a player's best interest to be the opposite of his neighbors. That distinction changes the patterns of cooperators and defectors that arise. In Hauert and Doebeli's computer simulations of the snowdrift game, cooperators tend to form long tendrils, instead of the clumps observed in the prisoner's dilemma. The upshot is that the cooperators are exposed to exploiters even more than if the population mixed freely.

"There's a common belief that any form of spatial structure will promote cooperation," Hauert says. "We're challenging that."

Nowak says that Hauert and Doebeli are right to encourage game theorists to examine the snowdrift game more closely. "I've always had the perspective that the prisoner's dilemma is the only game where you could possibly talk about cooperation," he says. "Their approach has made me revise that perspective."

Ultimately, a better understanding of the interplay between cooperation and exploitation could help explain the emergence not just of cooperation but also of life itself. After all, life owes its origins to primeval acts of inanimate cooperation, in which RNA, proteins, and other molecules banded together to form cells.

"Whenever nature achieves a major step, it involves cooperation," Nowak says. ■